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CO-OSCILLATION AND SYNCHRONIZATION BETWEEN THE POSTERIOR THALAMUS AND THE CAUDATE NUCLEUS DURING VISUAL STIMULATION

P. GOMBKÖTő, A. BERÉNYI, T. NAGYPÁL, G. BENEDEK, G. BRAUNITZER AND A. NAGY*

Department of Physiology, Faculty of Medicine, University of Szeged, Dóm tér 10, H-6720 Szeged, Hungary

Abstract—Recent results suggest significant cross-correlation between the spike trains of the suprageniculate nucleus (SG) of the posterior thalamus and the caudate nucleus (CN) during visual stimulation. In the present study visually evoked local field potentials (LFPs) were recorded simultaneously in the CN and the SG in order to investigate the coupling between these structures at a population level. The effect of static and dynamic visual stimulation was analyzed in 55 SG–CN LFP pairs in the frequency range 5–57 Hz. Statistical analysis revealed significant correlation of the relative powers of each investigated frequency band (5–8 Hz, 8–12 Hz, 12–35 Hz and 35–57 Hz) during both static and dynamic visual stimulation. The temporal evolution of cross-correlation showed that in the majority of the cases the SG was activated first, and in approximately one third of the cases, the CN was activated earlier. These observations suggest a bidirectional information flow. The most interesting finding of this study is that different frequency bands exhibited significant cross-correlation in a stimulation paradigm-dependent manner. That is, static stimulation usually increased the cross-correlation of the higher frequency components (12–57 Hz) of the LFP, while dynamic stimulation induced changes in the lowest frequency band (5–8 Hz). This suggests a parallel processing of dynamic and static visual information in the SG and the CN. To our knowledge we are the first to provide evidence on the co-oscillation and synchronization of the CN and the SG at a population level upon visual stimulation, which suggests a significant cooperation between these structures in visual information processing.

Key words: caudate nucleus, suprageniculate nucleus, local field potential, cross-correlation, cat.

INTRODUCTION

Although the caudate nucleus (CN) is strongly involved in the control of visually guided oculomotor and skeletomotor functions (Lynd-Balta and Haber, 1994; Barneoud et al., 2000; Hikosaka et al., 2000) there is some uncertainty concerning the pathways conveying sensory information to the striatum. The first morphological findings in cats and rabbits suggested the geniculo-striate pathway (Webster, 1965; Hollander et al., 1971), however, more recent studies support the assumption that the ascending tectofugal system also projects to the CN in amniotes. This information can be critical for the normal sensory-motor function of the CN (Nagy et al., 2006). It is known that the CN is anatomically connected to the extrageniculate visual and intralaminar thalamic nuclei but not to the dorsal lateral geniculate body (LGNd) (Harting et al., 2001). The visual associative cortex along the anterior ectosylvian sulcus of the feline brain also projects to the CN (Nagy et al., 2011). Furthermore, an electrophysiological study is available (Rokszin et al., 2011), which suggests a direct functional connection between the thalamic relay nucleus (suprageniculate nucleus (SG) of the posterior thalamus) of the ascending tectofugal system and the CN. In this study the temporal relations of simultaneously recorded SG and CN neuronal spike trains were investigated.

The bidirectional and parallel connections between the structures of the visual system in the mammalian brain (Stone et al., 1979; Lennie, 1980; Ogasawara et al., 1984; Hashemi-Nezhad et al., 2003; Rokszin et al., 2011) provide an alternative to the serial information transmission described earlier in the geniculo-striate visual system (Hubel and Wiesel, 1962, 1965). Apart from the recognition of numerous parallel channels there is also substantial evidence to indicate that feedback projections from the extrastriate cortices exert influence on the receptive field properties of neurons in the primary visual cortices (Wang et al., 2000; Bullier et al., 2001; Huang et al., 2007).

The ascending tectofugal system a parallel pathway beside the geniculo-striate one may be regarded as the remnant of an ancient visual system, which, in higher animals, plays a role mostly in the control of motion, novelty detection and eye movements. However, how rapid sensory information (spatial visual coordinates) necessary for the realization of actual motor patterns is transmitted to those parts of the basal ganglia which participate in the modulation of eye movements

*Corresponding author. Address: Department of Physiology, University of Szeged, Dóm tér 10, P.O. Box 427, H-6720 Szeged, Hungary. Tel: +36-62-545869; fax: +36-62-545842.
E-mail address: nagy.attila.1@med.u-szeged.hu (A. Nagy).

Abbreviations: CN, caudate nucleus; EEG, electroencephalogram; FFT, Fast Fourier transformation; LFP, local field potential; MAC, minimum alveolar anesthetic concentration; PSD, power spectral density; SG, suprageniculate nucleus.

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(Hikosaka et al., 2000) remains unanswered. To find an answer to this question we sought evidence for a functional relationship between the CN and SG.

EXPERIMENTAL PROCEDURES

Preparation of experimental animals

Experiments were performed on five adult cats of either sex, weighing between 2.5–4 kg. All experimental procedures were carried out to minimize the number of the animals involved and followed the European Communities Council Directive of 24 November 1986 (86609 EEC) and the National Institutes of Health guidelines for the care and use of animals for experimental procedures.

The animals were initially anesthetized with ketamine hydrochloride (Calypsol, 30 mg/kg i.m.). To reduce salivation and bronchial secretion, a subcutaneous injection of 0.2-ml 0.1% atropine sulfate was administered preoperatively. After cannulation of the femoral vein and the trachea, animals were placed in a stereotaxic headholder. All wounds and pressure points were treated regularly with local anesthetic (1%, procaine hydrochloride). Throughout the surgery the anesthesia was continued with halothane (Halothane, 1.6%) in air. The animals were immobilized with an initial 2-ml intravenous bolus of gallamine triethiodide (Flaxedil, 20 mg/kg), and artificial ventilation was introduced. During recording sessions, a mixture containing gallamine triethiodide (8 mg/kg/h), glucose (10 mg/kg/h) and dextran (50 mg/kg/h) in Ringer lactate solution was infused continuously at a rate of 4 ml/h. The eye contralateral to the subcortical recording site was treated locally with atropine sulfate (1–2 drops, 0.1%) and phenylephrine hydrochloride (1–2 drops, 10%) to dilate the pupils and block accommodation and to retract the nictitating membranes, respectively, and was equipped with a +2 diopter contact lens. The ipsilateral eye was covered during stimulation and recordings. During the recording session, anesthesia was maintained with a gaseous mixture of air and halothane (1.0%). The depth of anesthesia was monitored by continuously checking the end-tidal halothane concentration and by monitoring heart rate (electrocardiogram) and brain activity (electroencephalogram, EEG). By adjustment of the concentration of halothane, high-amplitude, slow-frequency EEG activity with sleep spindles could be maintained. We also checked repeatedly whether any of the experimental procedures or a forceful pressing of the forepaws might induce desynchronization. The minimum alveolar anesthetic concentration (MAC) values calculated from the end-tidal halothane readings were kept in the range given by Villeneuve and Casanova (Villeneuve and Casanova, 2003). The end-tidal halothane concentration, MAC values and the peak expired CO_2 concentrations were monitored with a capnometer (Capnomac Ultima, Datex-Ohmeda, Inc., USA). The O_2 saturation of the capillary blood was monitored by pulse oxymetry. The peak expired CO_2 concentration was kept within the range 3.8–4.2% by adjustment of the respiratory rate or volume. The body temperature of the animal was maintained at 37 °C by a warm-water heating blanket with an automatic control. Craniotomy was performed with a dental drill to allow a vertical approach to the target structures. The dura mater was preserved, and the skull hole was covered with a 4% solution of 38 °C agar dissolved in Ringer's solution.

Recording and visual stimulation

Local field potentials (LFPs) were simultaneously recorded with tungsten microelectrodes (A-M Systems, Inc., USA) with an impedance of 2–4 MΩ. Vertical penetrations were made within Horsley–Clarke coordinates anterior 4.5–6.5 and lateral 4–6.5 for SG recordings at stereotaxic depths between 16–18 mm, while for CN recordings were between the co-ordinates anterior 12–16 and lateral 4–6.5, at stereotaxic depths between 12 and 19 mm. Microelectrodes were advanced with a microstepper. Electrical signals were conventionally amplified, displayed on an oscilloscope and transformed through a loudspeaker.

For visual stimulation random dot kinetograms were utilized consecutively in each trial. The stimuli consisted of 200 white dots, and in the dynamic condition these were moving at a speed of 5°/s. The diameter of each dot was 3 pixels (8.6 min of arc). These random dot kinetograms were generated in the Psychophysics Toolbox extension of Matlab® (Brainard, 1997; Pelli, 1997), and presented on an 18-inch computer monitor (refresh rate: 85 Hz) placed at a distance of 42.9 cm in front of the animal. The steady-state luminance of a stationary dot was 10 cd/m^2, while the background luminance was 2 cd/m^2. The stimulation sequence consisted of three phases: first, 1500-ms spontaneous activity was recorded with no stimulation; then, for another 1500 ms, random stationary dots were presented; finally, the same dots were moving for an additional 1500 ms. This sequence was repeated 500 times.

Data analysis

The analysis was performed on 55 recording site pairs. Two hundred ms-long segments were selected from six conditions for the analysis and comparison of LFPs. The conditions were: spontaneous activity, onset of static stimulus, static stimulus, onset of dynamic stimulus, dynamic stimulus, and stimulation offset. Frequency decomposition was performed on each trial. Four different frequency ranges were used. The first range was between 5–8 Hz, in the theta band, the second one was between 8–12 Hz, in the alpha band, the third one was 12–35 Hz in the beta band, and the last one between 35–57 Hz in the low gamma band. To measure the relation between oscillatory spindle co-occurrence at both sites (i.e. concomitance) the following method was used: the percent energy contribution of each of the four frequency bands was determined in the CN and SG as compared to the energy of the whole spectrum. This was done 500 times in all conditions. In this way 500 point pairs were obtained upon which a regression line was superimposed. Concomitance coefficient was defined as the value of any point along this line, and it was utilized to characterize the extent of the co-oscillation of the LFPs.

For the time resolved frequency decomposition of the LFPs the Fast Fourier transformation (FFT) was used. Each trial was analyzed separately using the following equation:

$$\mathrm{FFT}\%_N = \left(\frac{\int_{f1}^{f2} f(\mathrm{PSD}) d(\mathrm{PSD})}{\int_{f3}^{f4} f(\mathrm{PSD}) d(\mathrm{PSD})} \times 100) \right)_N$$

where f_1–f_2:5–8 Hz; 8–12 Hz; 12–35 Hz; 35–57 Hz; f_3 = 5 Hz; f_4 = 57 Hz, N = number of trials, PSD = power spectral density.

This yields an estimate of the tightness of correlation in oscillatory content between the two electrodes in a stationary condition. For these comparisons *t*-tests were used.

We also calculated the cross-correlation coefficient as a measure of synchronization between the two LFPs (Murthy and Fetz, 1996; Courtemanche and Lamarre, 2005). In contrast to the quantification of similarity in oscillatory profiles, this is a way to estimate the degree of simultaneous change in the recorded signals (Roelfsema et al., 1997; Gerstein, 2008). We used a moving window of 200 ms. This window moved with a 100-ms overlap over the LFPs. LFP cross-correlation coefficients across these windows were calculated to analyze synchronization. Cross-correlation coefficients from all six periods of stimulation were compared using *t*-test.

RESULTS

Oscillations between the SG and CN

Fifty-five recording site pairs were simultaneously recorded from the CN and the SG (Fig. 1).

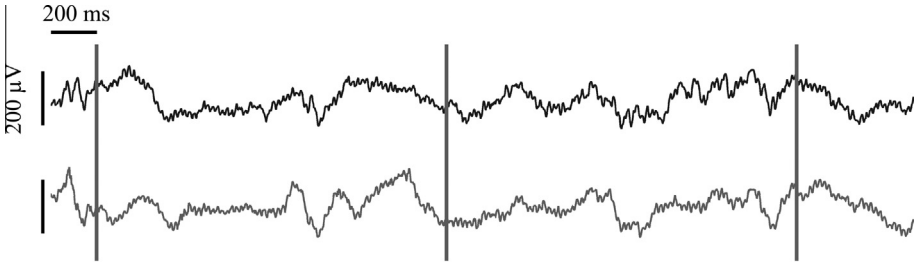

Fig. 1. Simultaneous LFP recordings from the caudate nucleus (CN) and the suprageniculate nucleus (SG). The figure shows trials of LFPs simultaneously recorded in the CN (black) and the SG (gray), respectively during visual stimulation. Vertical gray lines indicate the duration of visual stimulation. In the first 1500-ms period (between the first and the second gray lines) static visual stimulation was applied while in the second period of the same length (between the second and third gray lines) dynamic visual stimulation was used. The horizontal and vertical scale bars show the time and voltage dimensions. Note the strong co-oscillation of the LFPs recorded simultaneously from the CN and the SG.

The degree of oscillatory co-occurrence was determined within the six 200-ms windows. Measurements were done in all the four frequency bands described above (see Experimental procedures). This way it was possible to show if changes in the percent energy contribution of a given band within the LFP recorded from one structure was linked to changes in the percent energy contribution of the frequency components of the LFP of the other structure. This relation was characterized by a concomitance value. With the help of the six windows it was possible to find out about how concomitance was related to the phases of stimulation (see Fig. 2).

Synchronization between SG and CN

After establishing concomitance, we also investigated the continuous LFPs. We sought to find out if there was any temporal connection of event-related LFPs between the two structures. For this purpose the moving-window cross-correlation analysis was used. As an illustration, one SG–CN pair is given (Fig. 3).

Lag time was defined as the temporal position of the maximum value of the correlation coefficient in the entire interval. In 30 cases (55%) the cross-correlation coefficient had a positive value (mean time lag 16.2 ms ± 2.7), which means that the SG was activated earlier. In 19 site pairs (35%), the maximum of the coefficient had a negative value (mean time lag: −19.6 ms; ±3.24 ms) in each frequency band. It means that in these cases the CN was activated earlier. The comparison of absolute values of time lags revealed no significant difference between these two populations (Mann–Whitney U test, $p > 0.05$). Additionally there was no difference among the time lags of different frequency bands (one-way ANOVA analysis, $p > 0.05$). In the remaining six cases (10%) the activation was synchronous, with zero time lag.

Fig. 4 shows the mean population cross-correlation coefficients of CN–SG LFP pairs in each segment of visual stimulation. The changes in cross-correlation upon visual stimulation compared to cross-correlation of spontaneous activities were analyzed. It can be seen that LFPs recorded from both structures filtered for different frequency bands exhibited significant cross-correlation in a stimulus-dependent manner. Between the CN–SG LPP pairs we found significant ($p < 0.05$) changes in the theta-band upon the onset of the static stimulus ($r = 0.64$,) upon the onset of the dynamic stimulus ($r = 0.57$) and upon stimulation offset ($r = 0.49$). In the alpha-band cross-correlation changed significantly upon stimulus offset. ($r = 0.6$). In the beta-band a significant change of cross-correlation was observed during static stimulation ($r = 0.44$), while in the gamma band the change was significant upon the onset of the static stimulus ($r = 0.56$).

DISCUSSION

In the present study we sought to prove the existence of information transfer between the CN and the ascending tectofugal system. LFPs recorded simultaneously from the CN and SG were used. SG is a thalamic relay nucleus, which is assumed to transmit visual information from the superior colliculus toward other structures of the ascending tectofugal system (Norita and Katoh, 1986; Katoh et al., 1995; MacNeil et al., 1997; Harris et al., 2000; Guirado et al., 2005), and also to the CN (Harting et al., 2001). In an earlier study Rokszin et al. (2011) investigated and analyzed the interaction between the SG and CN at the single-cell level. The study used cross-correlation methods to provide the first piece of direct evidence on the functional connection between the SG and CN. It was also described earlier that drifting sinewave gratings could modulate the responses of a significant proportion of the CN neurons. At the same time it is known that afferentation originating from the superior colliculus and the SG is mostly weakly modulated or unmodulated (Paróczy et al., 2006; Waleszczyk et al., 2007; Márkus et al., 2009). It may be assumed, therefore, that CN neurons that exhibit weak modulation or no modulation at all receive unmodulated visual information from the SG, while CN neurons showing modulated responses receive afferentation from the AES cortex (Hicks et al., 1988; Nagy et al., 2011), an area of strong temporal frequency modulation.

In the present study we analyzed the oscillation and synchronization between the CN and SG using simultaneously recorded LFPs, which allowed us to check for the existence of communication between the

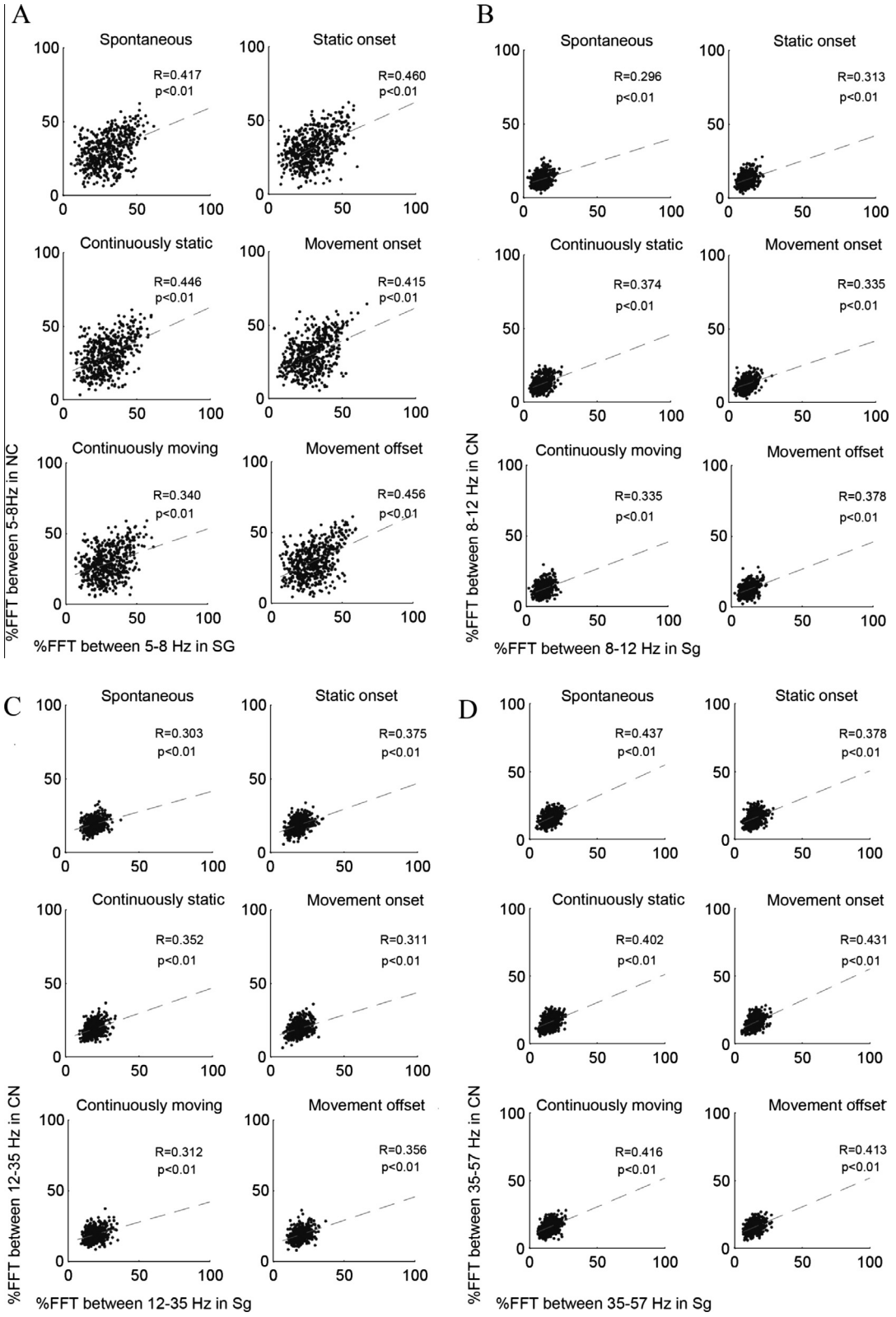

Fig. 2. Oscillation between the CN and the SG. Relationship between the 5–8 Hz (Part A), 8–12 Hz (Part B) 12–35 Hz (Part C) and 35–57 Hz (Part D) oscillatory contents (FFT%) of the LFP signal (see Experimental procedures for the details of calculation). The six subplots show the oscillatory content during the six different segments of the stimulation: (1) spontaneous activity, (2) onset of static stimulus, (3) static stimulus, (4) onset of dynamic stimulus, (5) dynamic stimulus, and (6) stimulation offset. Correlation coefficients (*R*) show the strength and direction of the linear relationship between two structures. Dashed lines are regression lines. Note the strong co-oscillation between the CN and the SG in each frequency range and also during each segment of visual stimulation.

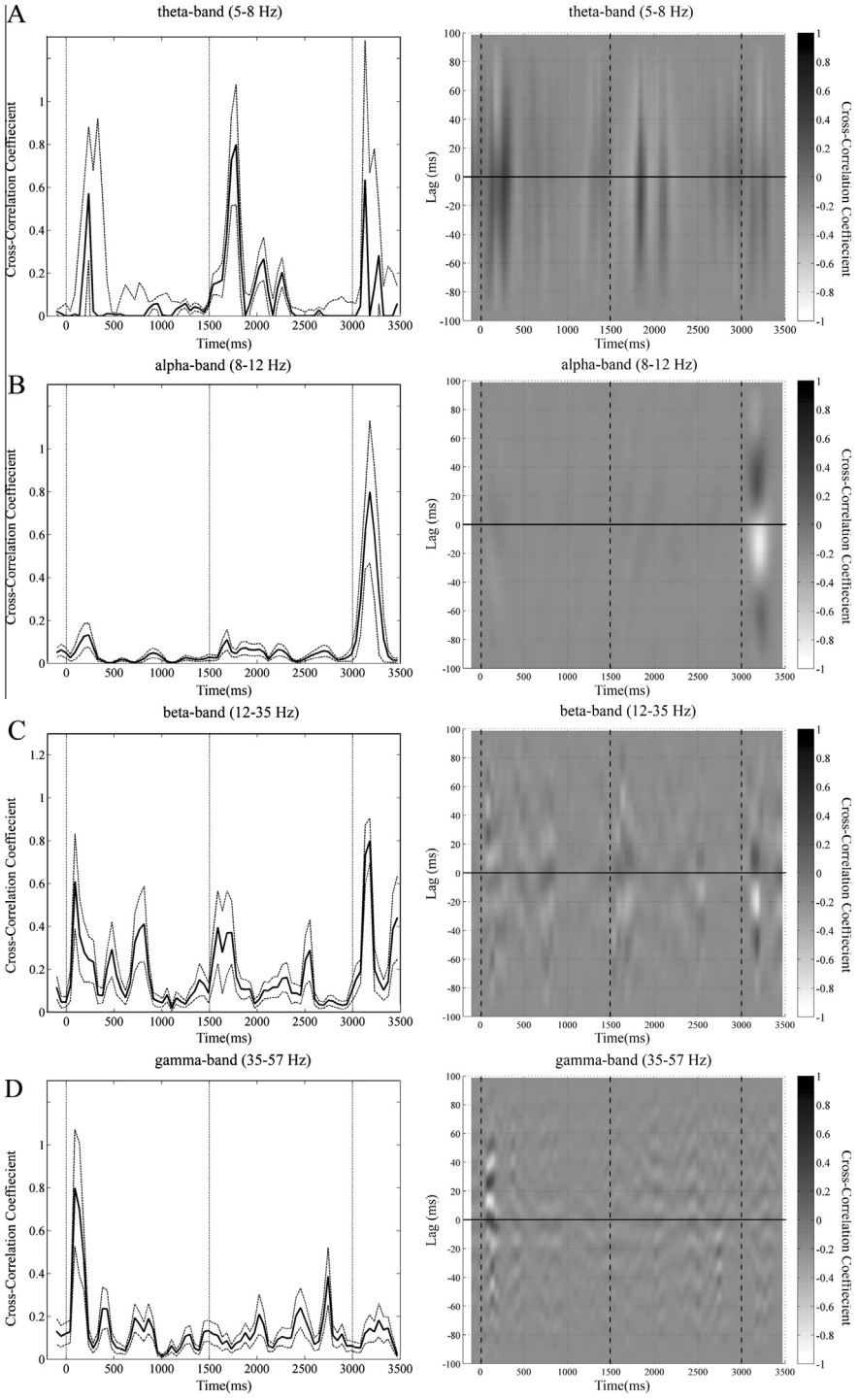

Fig. 3. The temporal evolution of LFP cross-correlation between the SG and the NC during visual stimulation. Subplots on the left side show mean of the temporal evolution of cross-correlation (500 trials). Subplots on the right side show the mean cross-correlation coefficient (black line) and ±2 SD (dashed lines) at maximum time lag in the four frequency ranges. Lag time was defined as the temporal position of the maximum value of the correlation coefficient in the entire interval. Part A shows the temporal evolution of cross-correlation coefficient during stimulation in the 5–8-Hz range. Part B shows the temporal evolution of cross-correlation coefficient during stimulation in the 8–12-Hz range. Part C shows the temporal evolution of cross-correlation coefficient during stimulation in the 12–35-Hz range. Part D shows the temporal evolution of cross-correlation coefficient during stimulation in the 35–57-Hz range. The vertical dashed lines delimit the different epochs of the stimulation. Between the first and the second dashed line (1500 ms) static visual stimulation was used while between the second and third dashed line (1500 ms) dynamic stimulation was applied.

SG and CN at a population level. We analyzed the power of various frequency bands of the two structures and investigated the relationship between the ''co-oscillating'' NC and SG populations during visual stimulation.

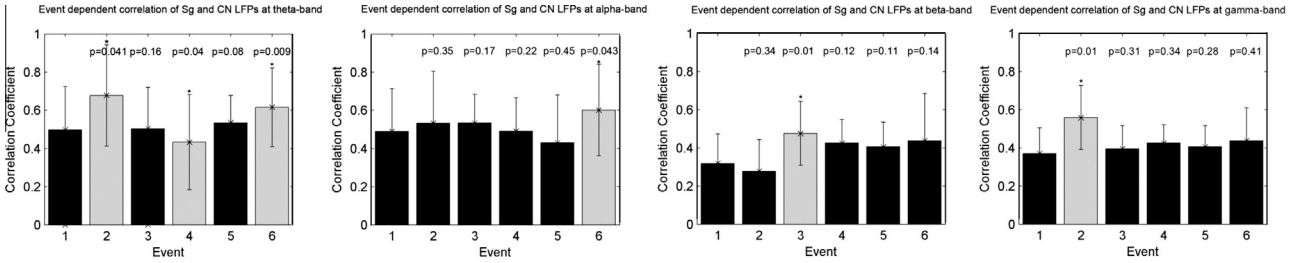

Fig. 4. Mean population cross-correlation coefficients of CN–SG LFP pairs in each segment of visual stimulation. The bars represent the cross-correlation coefficients during the six segments of the stimulation (similarly to Fig. 2). Gray bars denote significant difference of cross correlation in a particular epoch of visual stimulation during spontaneous activity. Note that mainly the phasic events of stimulation (onset of moving stimulus and stimulation offset) changed the cross-correlation significantly between the CN and SG in the theta band (5–8 Hz) (Part A). Beta (12–35 Hz) and gamma (35–57 Hz) band components (Part C and Part D) showed significant changes only during tonic stimulation. Significant change in the alpha band (8–12 Hz) (Part B) was found only upon stimulus offset.

Several cortical areas have specific oscillation patterns with well-defined physiological functions, such as the prefrontal cortex with its 4-Hz oscillation, or the 7–11-Hz hippocampal oscillation (Fujisawa and Buzsáki, 2011). Recently, these oscillations have received more attention from the aspect of synchronization and information transfer. There is great emphasis on the investigation of the importance of phase locking. It was for this reason that we examined interaction dynamics between the CN and SG. Our results suggest that there is a strong coupling between the structures, even without visual stimulation. The co-dependence of the relative power of the frequency ranges (concomitance coefficients) remains stable during every stimulation segment, which suggests that the visual stimulation does not decouple the thalamostriatal pathway. The analysis of the relative power of all investigated frequency bands (5–8, 8–12, 12–35, 35–57 Hz) in the LFP signals also showed coupling (co-oscillation) between the CN and SG neuron populations. The presence of the common frequency components during visual stimulation provides evidence on the information transfer between these two structures.

The temporal evolution of cross-correlation revealed when and in what order information transmission between the CN and SG occurs, and which frequency bands contain the most information in this crosstalk. In 55% of the cases the SG was activated first, while in 35% of the measurements CN activation occurred earlier. Thus it was not possible to determine unambiguously whether the SG or CN is the earlier stage of the information processing pathway. In cases when the SG is activated earlier, it seems to be the sender structure, and it sends the information toward the CN. This result is in line with earlier studies, which also suggested a thalamostriatal pathway in the amniotic brain (Takada et al., 1985; Hu and Jayaraman, 1986; Harting et al., 2001; Guirado et al., 2005; Hoshino et al., 2009). However, in several cases the CN is activated earlier. In these cases CN seems to be the sender, and it is supposed to be the information transmitter toward SG. This observation, similarly to the cross-correlation analysis at the single-cell level (Rokszin et al., 2011), suggests a bidirectional information flow between the posterior thalamus and the CN. However, in the remaining 10%, activation was synchronous, with zero time lag. As for this finding we assume that a common, synchronizing input might also exist, comprising of parallel pathways (Rokszin et al., 2011). The source of this common input might be the visual associative cortical areas, i.e. the anterior ectosylvian cortex or the lateral suprasylvian areas of the feline brain (Norita and Katoh, 1986). This common input hypothesis is supported by the existence of neurons with bifurcating axons, which are well-known and prevalent in the ascending tectofugal system (Katoh et al., 2000; Hoshino et al., 2004).

The most interesting finding of the present study is that LFPs recorded from both structures, filtered for different frequency bands, exhibit significant cross-correlation in a stimulus-dependent manner. In the theta-band (5–8 Hz) the onset of static stimulus, the onset of moving stimulus and stimulation offset resulted in significant changes of cross-correlation. In the beta-band (12–35 Hz) a significant change in cross-correlation was observed during static stimulation, while the gamma-band (35–57 Hz) showed significant change upon the onset of static stimulation. Thus, it can be concluded that tonic (static) stimulation increased the cross-correlation of the higher frequency (12–57 Hz) components of the LFP, while phasic (dynamic) stimulation resulted in changes in the lower frequency (5–8 Hz, theta band) signal. It is also worth mentioning that the alpha-band (8–12 Hz) exhibited change also upon the offset of the visual stimulus. The analysis of temporal evolution of cross-correlation suggests parallel processing of dynamic and static visual information between the posterior thalamus and the CN.

To our knowledge, we are the first to provide evidence on the co-oscillation and synchronization of the CN and the SG at a population level. Our results also suggest a functional cooperation between the CN and the ascending tectofugal system in visual information processing in the feline brain.

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